

## Morphology, architecture and taxonomy in the *Hebe* complex (*Scrophulariaceae*)

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**Summary** : Notes on morphology and classification in the *Hebe* complex are given, together with a new interpretation of the "whipcord" shrub habit of several sections of *Leonohebe*. It is suggested that shoot systems in these plants represent largely sterilised inflorescences, and that the foliage comprises sterile inflorescence bracts. This architecture is compared with that of ericoid and divaricating shrubs.

**Résumé** : La morphologie et la classification du complexe générique *Hebe* sont présentées, avec une interprétation nouvelle de l'architecture des arbustes à rameaux flagelliformes de plusieurs sections de *Leonohebe*. L'auteur suggère que les rameaux de ces plantes correspondent essentiellement à des inflorescences devenues stériles, et que leurs feuilles représentent des bractées stériles. Une telle architecture est comparée à celle des arbustes éricoïdes et divariqués.

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The tribe *Digitaleae* of *Scrophulariaceae* is one of the most diverse groups of flowering plants in New Zealand, where its members are important components of many shrublands. Problems in understanding the evolution and classification of the tribe in New Zealand have remained at subgeneric, generic and tribal levels ever since BENTHAM (1846) treated the entire group (apart from *Ourisia*) as a single section, *Hebe*, of the genus *Veronica*. Five genera are accepted here for the group in New Zealand, *Chionohebe*, *Leonohebe*, *Hebe*, *Parahebe* and *Ourisia* (Table 1). This paper examines morphology, especially plant architecture, and taxonomy in the group. Details on nomenclature and biogeography are given in HEADS (1987, 1992, 1993).

### TAXONOMIC HISTORY

**SUBFAMILIES** : THIERET (1967) has argued that the higher level taxonomy of *Scrophulariaceae* "is in a sorry state indeed" and that satisfactory subfamilies or even tribes are lacking. The subfamilies proposed by WETTSTEIN (1891) and still in general use to-day are characterised by modes of corolla aestivation : *Antirrhinoideae* have the adaxial ("posterior") corolla lobes outermost in bud, while *Rhinanthoideae* have the abaxial ("anterior") or lateral lobes outermost. But at least in certain cases this is a feature of little importance (DIELS, 1897 ;

ARMSTRONG & DOUGLAS, 1989). For example, *Lindenbergia* is generally accepted as *Antirrhinoideae*, but has the anterior corolla lobes external in the bud (HARTL, 1957), in the wrong position for that subfamily. Aestivation characters in *Ourisia*, *Leonohebe* and *Chionohebe* discussed in this paper also threaten WETTSTEIN's subfamilial divisions, or at least show interesting incongruence with them.

TRIBES : Tribal groupings in *Scrophulariaceae* also remain unresolved. For example, HONG (1984) used loculicidal (or loculicidal and septicidal) dehiscence as a synapomorphy for a tribe *Veroniceae*, even though he included here *Hebe* sensu lato and *Parahebe* which have mainly septicidal dehiscence. This seems unsatisfactory and the larger group Tribe *Digitaleae* sensu BAILLON (1888) and WETTSTEIN (1891) is used here rather than the smaller group *Veroniceae* in the sense of PENNELL (1921), HONG (1984) and others.

Within *Digitaleae*, *Hebe* s.l., *Chionohebe* and *Parahebe* were accepted by HONG (1984) as forming a monophyletic group, with *Detzneria* and then *Veronica* as sister groups. *Hebe*, *Parahebe*, *Chionohebe*, *Leonohebe*, *Detzneria* do seem to be closely related, and make up a " *Hebe* complex ", a term used here in a loose sense and for convenience only. The status and boundaries of the group remain as unclear as its position within *Scrophulariaceae*.

#### I. *Hebe* Commerson (1789).

Commerson (*in* DE JUSSIEU, 1789) described a new genus, *Hebe*, for a shrub of southern South America. The species and 26 others from New Zealand and Australia were treated as *Veronica* section *Hebe* by BENTHAM (1846) and WETTSTEIN (1891). PENNELL (1921) reinstated *Hebe* as a genus for the American plants, but like most authors did not realise the diversity of the group in New Zealand. For example, PENNELL described the flowers as " all in axillary racemes ", which is not true for many forms treated here in *Leonohebe*. COCKAYNE & ALLAN (1927) confused the situation by uncritically transferring many New Zealand species from *Veronica* to *Hebe*. Most authors currently follow ALLAN (1961) who used three genera, *Hebe* and two later segregates, *Chionohebe* and *Parahebe*, for this complex, but there has been continuing controversy over the delimitation of these genera. Characteristic of all accounts from those of BENTHAM and PENNELL through to current treatments, is a large, highly heterogeneous group *Hebe*. Possible problems were first hinted at by MOORE (1961) who referred to some plants usually placed in *Hebe* s.l. as " difficult to accomodate there ". Later, MOORE (*pers. comm.*, Jan. 1987) still felt that generic groupings in the complex required revision.

PHILLIPSON (1980) studied taxonomy and leaf surface anatomy in the *Hebe* complex and concluded that the generic concepts in the group are " in a confused state " and " must be abandoned ". He found that the group treated here as *Hebe* is " very homogeneous ", but still preferred a larger genus than this group. He also found that " in some ways [*Hebe* " group *Paniculatae* " of MOORE 1961 and *H. macrantha*] are more like species of *Parahebe* in the surface of their leaves ". PHILLIPSON suggested that *H. macrantha* (and *H. formosa*) should be removed from *Hebe* and placed in *Parahebe*, with which I agree. With respect to " group *Paniculatae* " he noted that the habit, and leaf and shoot morphology are " more similar to *Parahebe* than to most other species of *Hebe* ", but suggested a new genus for the group, which is not accepted here.

TABLE I : Character combinations in the *Hebe* complex.

	BRACTS	LEAF PAIRS	CHROMOSOME NUMBER (x)
<b>Chionohebe</b>	One pair : opposite, connate.	connate, chiasmatic pairs.	21
<b>Leonohebe</b> sect. :			
Densifoliae	all opposite and connate	connate	21
Leonohebe	"	connate	21
Connatae	"	connate	21
Apiti	"	connate	20
Flagriformes	"	connate	20
Aromaticae	"	± connate	21
Salicornioides	"	connate (no visible node)	21
Buxifoliae	"	usually connate	21
<b>Hebe</b>	Basal adaxial pair sometimes present, but pairing subsequently dirempted.	Leaves not connate, margins coherent until late.	20
<b>Parahebe</b>	not opposite	connate or not.	20 or 21

Although BENTHAM's (1846) delimitation of *Hebe* s.l. has remained largely unquestioned until now, a survey of biogeography and morphology in the group indicates that there are no characters on which *Hebe* s.l. can be maintained, either as a subgeneric group (BENTHAM, 1846, 1869; HOOKER, 1864; WETTSTEIN, 1891; CHEESEMAN, 1906) or a genus (PENNELL, 1921; COCKAYNE & ALLAN, 1927; ALLAN, 1961).

While *Hebe* s.l. must be abandoned, it can simply be replaced by two strongly characterised groups : *Hebe* in an emended, narrow sense, and *Leonohebe* (HEADS, 1987). These differ in their vegetative architecture, bud morphology, inflorescence structure, chromosome number (Fig. 1) and largely vicariant distribution patterns. Neither of the groups has been accepted at any rank in previous treatments. However, *Hebe* as here conceived has been referred to, more or less implicitly. HOOKER (1864) discussed 19 species of New Zealand *Veronica* among which he felt "it is most difficult to draw any contrasting specific characters, they appear to present a graduated scale of forms". This group (apart from *V. buxifolia*) comprises the genus *Hebe* in the narrow sense of this paper. MOORE (1961) referred to the same alliance as "the more typical species of *Hebe*", in which "the two leaves of an opposite pair do not diverge from one another until they are almost full-grown". Later MOORE (1967) depicted the group as monophyletic in a branching phylogenetic diagram.

## II. *Leonohebe* Heads (1987 : 4).

Members of this genus were formerly included in *Hebe* or *Chionohebe*. *Leonohebe* is more heterogeneous than *Hebe* or *Chionohebe* (Table 1), but the opposite and connate inflorescence bracts in all but one species make determinations straightforward. *Leonohebe* includes several striking monotypic or oligotypic sections, and while morphologically more diverse than *Hebe* it has fewer species. *Leonohebe* is related to *Hebe* through species such as *L. odora* and *H. pimeleoides*, and also to forms of both *Parahebe* and *Chionohebe*. *Leonohebe petriei*, with an unusual combination of characters, remains difficult to place. The three divisions of MOORE'S (1961) "group Flagriformes" accepted by PHILLIPSON (1980) are also supported here.

## III. *Chionohebe* Briggs & Ehrendorfer (1976).

Three species of cushion plants with distinctive phyllotaxis were separated by HOOKER (1864) from *Veronica* s.l. as *Pygmea*, later renamed *Chionohebe* by BRIGGS & EHRENDORFER (1976) to avoid confusion with *Pygmaea*, a lichen. The genus as accepted here is a very distinct group of five closely allied species.

## IV. *Parahebe* Oliver (1944).

The group of New Zealand plants later to be named *Parahebe* was allied with *Veronica* s.s. by CHEESEMAN (1925). This seems perceptive, although subsequently differences between the two have been stressed. *Parahebe* was allied by FRANKEL & HAIR (1937) with *Hebe* s.l. rather than with *Veronica* on the basis of chromosome number. This still seems to be the most reliable difference between the *Hebe* group, with  $x = 20$  or  $21$ , and *Veronica* with  $x = 7, 8$  or  $9$  (DARLINGTON & WYLIE, 1955; BRIGGS & EHRENDORFER, 1968). In addition, ALLAN (1940) noted that *Parahebe* and *Hebe* s.l. share mainly septicial capsule dehiscence, while *Veronica* fruits are loculicidal. Nevertheless, *P. cheesemanii*, for example, is "almost entirely loculicidal" (GARNOCK-JONES, 1975). GRAYER-BARKMEIJER (1978; unpublished data cited in HONG, 1984) pointed out differences between *Parahebe* and *Veronica* in the glycosides and flavonoids present. Finally, HONG (1984) separated the *Hebe* group from *Veronica* on the basis of the pulvinate leaf-base of the former group, although this structure is more varied than he implied.

*Parahebe* has in turn been distinguished from *Hebe* s.l. through the plane of capsule compression. OLIVER (1944), when naming the new genus, cited difference from *Veronica* in chromosome number and difference from *Hebe* in the laterally compressed capsule. ALLAN (1961 : 842) noted that the capsule of *Parahebe* is "laterally compressed or turgid and always more or less didymous", while the capsule of *Hebe* s.l. is described as "more or less dorsally compressed, occasionally [notably in *Leonohebe* sect. *Leonohebe*] strongly laterally compressed with narrow septum but then never didymous". However, *Leonohebe pauciflora* has the capsule laterally compressed and didymous (illustrated by EAGLE, 1982), and *L. cupressoides* has a more or less didymous capsule (ALLAN, 1961). *Chionohebe* also has a laterally compressed, didymous capsule. Even in *Hebe* s.s., *H. pinguifolia* has a more or less didymous

capsule (MOORE, 1961), and the capsule of *H. pareora* is “strongly didymous” (GARNOCK-JONES & MOLLOY, 1982). As ASHWIN (1961) warned, although OLIVER’s (1944) arrangement “has been accepted by most recent authors... the shape and dehiscence of the capsule do not in themselves distinguish *Parahebe* absolutely from the wide range of species at present included in *Hebe*, and there is more diversity in other characters than OLIVER’s brief description suggests...”. In the classification adopted here, less weight is given to characters of the fruit, and more to variation in the inflorescence.

New Guinea plants formerly treated in *Veronica* and *Hebe* were placed in *Parahebe* by VAN ROYEN & EHRENDORFER (1970). VAN ROYEN (1972) discussed this treatment and wrote that : “The two grooves along the lines of the septum give all capsules a distinct didynamous appearance. This detail is nowhere found in *Hebe*, and this clearly separates *Parahebe* from *Hebe*... *Parahebe* and *Hebe* differ mainly by the didynamous and laterally compressed capsule of *Parahebe* against the non-grooved and dorsally compressed capsule of *Hebe*. In the leaves also the incised margins in *Parahebe* differ from the entire margins of *Hebe*”. As indicated above, the situation with respect to capsule shape is more complex than VAN ROYEN realised. In *Leonohebe cheesemanii*, *L. tumida* and *L. epacridea* the ovary has a groove along the line of the septum and in the first two species is somewhat didymous. Septal grooves are also present in *Hebe* s.s. (for example in *Hebe pinguifolia* and *H. pareora*). Incised leaf margins are not restricted to *Parahebe* but also occur in many forms of *Leonohebe*, in *Hebe diosmifolia* and others. However, VAN ROYEN & EHRENDORFER’s placement of the New Guinea plants in *Parahebe* does seem correct, if for other reasons.

In certain Papua New Guinea *Parahebe* species the floral disc has a very distinct ciliate margin absent in *Chionohebe*, *Leonohebe* and *Hebe* s.s. and the New Zealand members of *Parahebe sensu* OLIVER (revised by GARNOCK-JONES, 1975). VAN ROYEN (1983) describes the ciliate margin of the floral disc in *P. giulianettii*. In *P. lendenfeldii* the disc is described as “glabrous”, but illustrated as ciliate. Also with ciliate discs are *P. rubra* and *P. diosmoides*. The lax, paniculate inflorescences of *P. lendenfeldii* and *P. giulianettii* also resemble those of the New Zealand *Hebe* “group *Paniculatae*”. These Papua New Guinea species are probably related (VAN ROYEN, 1972), and are all found in the east of the country, disjunct between Huon Peninsula and the sector : Mt Albert Edward-Mt Kenive. This group shows direct affinities with the New Zealand *Hebe* “group *Paniculatae*”, the only related group sharing a ciliate disc (pers. obs.) and also sharing similar habit and inflorescence. These New Zealand and New Guinea ciliate-disc plants probably belong with other members of *Parahebe*.

If *Parahebe* is thus taken to include the usual species (ALLAN, 1961), plus the several New Guinea species, plus *Hebe* “*Paniculatae*” and finally *Hebe macrantha*, it forms a group characterised by lax inflorescences, with spiral bracts like *Hebe* s.s., but with variable chromosome number.

Some ten Australian species also appear to belong here. One of these, *P. lithophila*, is closely allied to New Zealand species of *Parahebe* (group A, below), and is retained in *Parahebe* by BRIGGS & EHRENDORFER (1992). According to BRIGGS & EHRENDORFER (1992) eight other Australian species comprise a group characterised by hairs in the corolla throat. They treat this group as a genus, *Derwentia*. The group may be monophyletic, but the character occurs elsewhere in *Hebe* s.s. (Chatham Is. and Rapa I. species) and a broader concept of *Parahebe* seems to me more useful. *Derwentia* is accepted here, informally, as a subgeneric group. BRIGGS & EHRENDORFER suggest that *P. formosa* of Tasmania and the New Guinean species may form

two more new genera, but because of their inflorescence these are also treated here within a broad *Parahebe*, which is more or less equivalent to BRIGGS & EHRENDORFER's " *Parahebe* clade ".

In her treatment of New Zealand *Parahebe*, ASHWIN (1961) proposed a " group A ", including *P. catarractae*, the type species, and three others, in which the lateral corolla lobes are folded around the stamens (cf. EAGLE, 1975, 1982; GARNOCK-JONES, 1975, 1976*b*). This character is not found in other South Pacific *Digitaleae*, but the folding of corolla lobes around internal organs in these genera is more widespread than has been reported. For example, the anterior corolla lobe is folded around the style in *Leonohebe* sects. *Buxifoliatae* (HEADS, 1992) and *Flagriformes* (see *L. hectorii* below) and in *Hebe brachysiphon*, *H. albicans*, and *H. barkeri* (DELPH, 1988). Such folding seems of little use in delimiting genera, but may be of use subgenerically, as with ASHWIN's *Parahebe* " Group A ".

The New Zealand *Parahebe birleyi*, *P. trifida* and their allies with very reduced inflorescences may prove to be better placed in *Leonohebe*.

#### V. *Ourisia* Commerson ex Juss. (1789).

*Ourisia* comprises some fourteen species of North, South and Stewart Is. of New Zealand, a single species of Tasmania, and twelve species of South America ranging north along the Andes to southern Ecuador (ARROYO, 1984). Its relationships are obscure, and at least several species have the " wrong " aestivation characters for the subfamily it is usually placed in (see below). *Ourisia* also displays a disconcerting recombination of characters at tribal level, having the united stigmas of the *Veroniceae* *emend.* THIERET but the divaricate anther cells of *Digitaleae* *emend.* THIERET (THIERET, 1967). Further study is required to elucidate the affinities of *Ourisia* which appear to be diffuse and complex. HALLIER (1903) even advocated transferring certain species of the genus to the *Gesneriaceae*.

## MORPHOLOGY OF NEW ZEALAND DIGITALEAE

### 1. HABIT AND ARCHITECTURE.

The erect shrub form, with all shoots orthotropic, is widespread in the group, and a few species form trees with distinct, erect trunks. Axis plagiotropy, identified by HALLÉ et al. (1978) as a key feature of tree architecture, is also present in the group. Many members develop prostrate shoot axes which may be woody or herbaceous, and these plants form mats, cushions, shrubs, or trees with prostrate trunks. *Hebe parviflora* var. *arborea*, *H. decumbens*, *H. buchananii*, *H. dieffenbachii*, *H. chathamica* and *H. insularis* all may have a prostrate trunk, equivalent to the " truncus superficialis " of some African *Dendrosenecio* (*Compositae*) (MABBERLEY, 1986). Similarly, the semi-lianoid *Hebe* group " *Paniculatae* " (MOORE, 1961) has sigmoid shoot axes which are prostrate basally, then erect, and distally plagiotropic. In members of *Hebe* sect. *Subdistichae*, especially *H. vernicosa*, all shoots tend to be more or less

plagiotropic but are not rooting. Plants of most *Leonohebe* species have at least some prostrate, rooting stem axes. *Leonohebe odora* has flowering shoots plagiotropically flexed distally. *Leonohebe* sect. *Flagriformes* has non-flowering plagiotropic long shoots, and flowering orthotropic short shoots. Finally, plagiotropy is most fully developed in the anisophyllous, dorsi-ventral shoots of *Ourisia glandulosa* and *O. caespitosa*.

COCKAYNE (1912) noted that in New Zealand the plagiotropic (prostrate) habit is especially common in plants of both coastal areas and subalpine moor and steppe. He also showed that the plagiotropic shoots of *H. chathamica* are irreversibly so. Shoots planted vertically in a pot quickly assumed the horizontal direction.

Apical meristems of orthotropic shoots are more or less circular in transverse section, with equal growth in the different sectors. If growth in a sector of the circle is reduced or even suppressed totally, the shoot will grow in a curve. Thus plagiotropy can be interpreted as the result of elimination of longitudinal growth sectors during evolution of the modern shoot. This process evidently involved suppression of parts and reduction in symmetry mode, from higher phyllotactic modes eventually down to 2-fold or bilateral (plagiotropic) symmetry (CROIZAT, 1961).

Within the *Hebe* complex, plagiotropic shoots of prostrate forms generally develop adventitious roots. Suppression of these roots is more or less complete in the many species of *Hebe* where all shoots are orthotropic, but even here suppression may be lifted by the application of biosynthetic inhibitors of gibberellins. HORRELL (1987 : Plate 4, 4) has illustrated treated plants of *Hebe* aff. *salicifolia* with dense clumps of aerial roots up to 3 cm long emerging near the shoot apices, recalling the prolifically rooting stems of cushion plants in *Chionohebe*.

The more or less woody, hard, cushion sub-shrub is a very distinctive growth form, and occurs in several species of *Chionohebe*. ASHWIN (1961) noted that the cushion-forming species of *Chionohebe*, with their small, salverform flowers and hairy leaves, are easily confused in the field with the similar cushions of certain *Myosotis* species (*Boraginaceae*). In particular, *C. myosotoides* resembles *M. pulvinaris*, and *C. pulvinaris* resembles *M. uniflora*. These ecological and morphological parallels correlate with the phylogenetic affinities between Scrophulariales (*Scrophulariaceae*, *Gesneriaceae*, etc.) and Polemoniales (*Solanaceae*, *Boraginaceae*, *Hydrophyllaceae*, *Polemoniaceae*, etc.), shown, for example, by the hairs of *Scrophulariaceae* which often have a basal cystolith as in *Boraginaceae* (CRONQUIST, 1981). The architecture of the small, very tight cushion species of *Chionohebe* is basically similar to that of larger, looser, cushion-like shrubs such as *Leonohebe propinqua* and the *Hebe traversii* complex.

## 2. PHYLLOTAXIS.

Phyllotaxis in the *Hebe* complex is generally decussate, with a trend towards distichy sometimes seen in plagiotropic shoots (e.g. *Hebe* sect. *Subdistichae*). However, HOOKER (1864) noted that in *Pygmaea* (now *Chionohebe*, unlike *Veronica* s.l., “The leaves appear to be imbricated all round the stem, and not opposite”. ASHWIN (1961) described the leaves as “irregularly imbricated”. The nature of this “irregularity” has never been analysed but is very distinctive (Fig. 1, a; photograph in RATKOWSKY & RATKOWSKY, 1974) and is the same in all five species accepted here for *Chionohebe*. In fact, the leaves are on orthotropic axes in

connate but “twisted” pairs, so that the decussate leaf arrangement so obvious in *Hebe* and *Leonohebe* is not evident. The phyllotactic pattern seen in *Chionohebe* has been described by CROIZAT in an analysis of phyllotaxis in *Helianthus*, in which “decussation tends to be distorted away from parameters at 90° into a disposition reminiscent of the letter X. A disposition of the kind — which I will henceforth designate as chiasma — is the rule in a very large number of plants though often cryptic and so easily overlooked” (CROIZAT, 1961 : 707). LOISEAU (1969) also viewed “bijugation” as “less rare than misunderstood”, and noted its presence in ferns and gymnosperms as well as in angiosperms. CROIZAT (1961) discussed and illustrated “chiasmata” in *Opuntia* (Fig. 87, c), *Bauhinia* (Fig. 93, c), *Lotus* (Fig. 94, a4), *Epilobium* (Fig. 100, b3), *Zea* (p. 827), *Succisa* (Fig. 102, b), *Mesembryanthemum* (p. 852), *Pinus* (Fig. 119, b), *Ceratopteris* (Fig. 147, a2), *Gnetum* (Fig. 170) and *Crassula* (CROIZAT, 1973, Fig. 11, d). The phyllotaxis of *Chionohebe* resembles that of succulent plants such as *Pterocactus kunzii*, as illustrated by BILHUBER (1933). BILHUBER made HIRMER’s “bijugy” the basis of a study of succulent plant phyllotaxis. His explanation of such “bijugate” patterns proposed a derivation from a hypothetical “Konstruktion” which had “unfavourable utilisation of space... without halving of the divergence angle”, to the actual system of “favourable utilisation space... with halving of the divergence angle”. Although this “splitting” theory was accepted in the influential work of SINNOTT (1960), it was criticised by CROIZAT (1961) who put into question the concept of “bijugy” on which BILHUBER’s and many subsequent analyses have been based. CROIZAT analysed this sort of phyllotaxis with reference to the structure of the chiasma and to lines of growing points, and demonstrated that “bijugate” systems are structurally intermediate between decussate/whorled systems and spiral systems of the same phyllotactic series. HENSLOW (1876) showed clearly how spiral phyllotaxis may develop from opposite and decussate systems. Chiasmatic phyllotaxis is shared by all species of *Chionohebe*, which are also linked very closely by their solitary, salverform flowers (Fig. 2, C1).

### 3. LEAF-BASE AND CORTEX.

The nature of the leaf-base (= leaf-cushion, podarium, *soubassement foliaire*, etc.) in *Leonohebe* (Fig. 1, b, c, d) is problematic, and has hardly been studied. HOOKER (1844) described this structure in *Veronica [Leonohebe] odora* as follows : “each [leaf] is jointed upon a thickening of the stem, which thickened portion appears like a broad petiole, united to the branch, and extending from the base of the true petiole to the leaf below, its edges almost meeting those of a similar thickening below the opposite leaf, but leaving a furrow between, which is covered with a fine pubescence [the “bifarious stem pubescence” of other authors]... in many, and in most species indeed [i.e. *Hebe* s.s.], the stem is incrassated below the leaf, but the thickened portion has not, as here, the appearance of a distinct body”. Like HOOKER, HONG (1984) was impressed by this “distinct body” and used the “pulvinus” of the leaf-base as a synapomorphy for the group : *Detzneria*, *Hebe* s.l., *Chionohebe* and *Parahebe*. However, a descriptive account of this interesting structure, let alone an analysis of its evolution, remains to be undertaken. Its morphology is more varied than HONG implies — for example, while the leaf-base of *Leonohebe* shows the well-marked development noted by HOOKER, the leaf-base is scarcely pulvinate in *Hebe*.



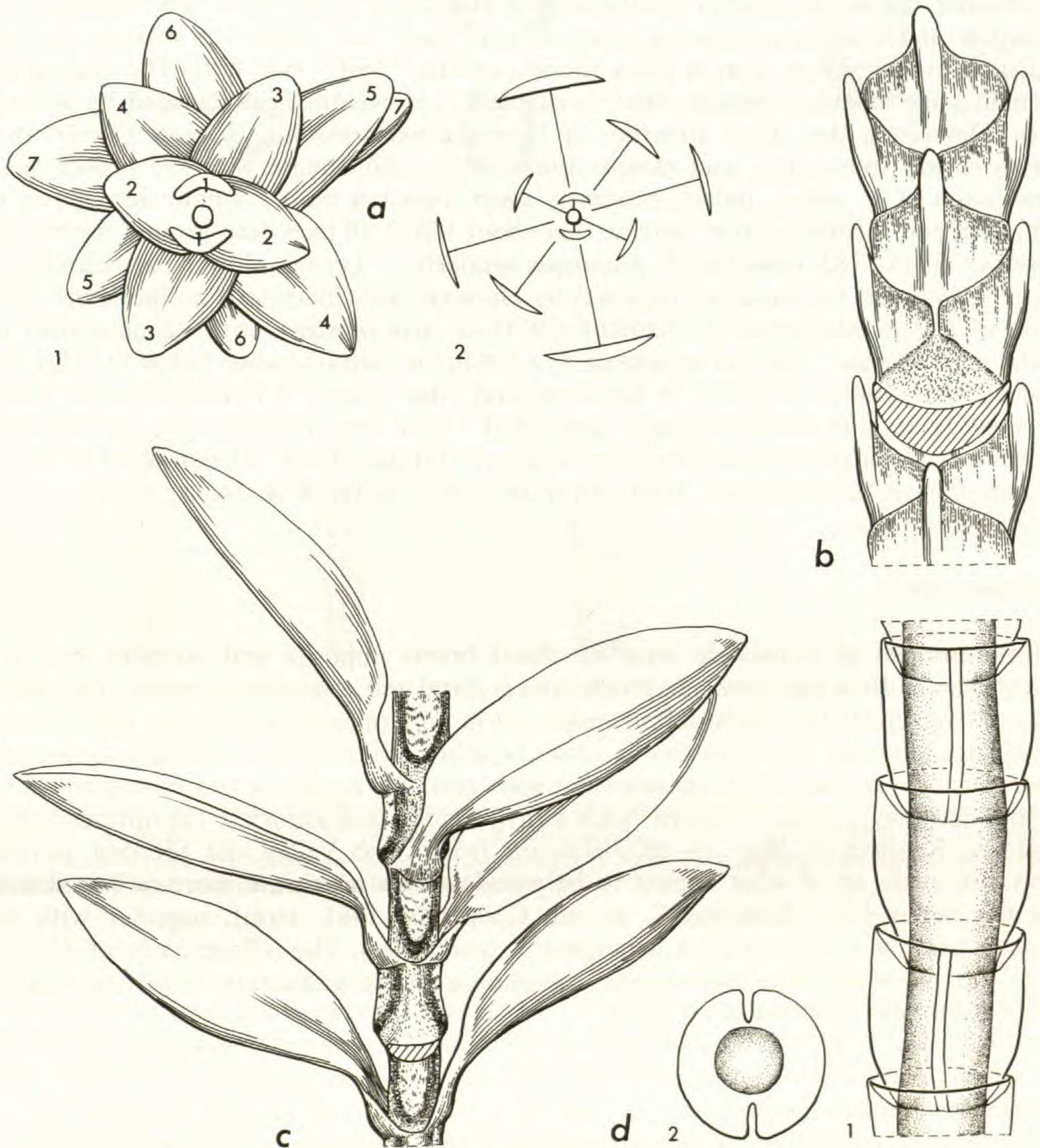


Fig. 1. — Aspects of shoot morphology in *Chionohebe* and *Leonohebe*. — a, *Chionohebe ciliolata* (Heads, 7.3.1987, OTA, Eyre Mts.) : 1, shoot ; 2, another shoot shown diagrammatically. — b, *Leonohebe lycopodioides* (Keogh, Heads, Tangney & Patrick, 12.1.1985, OTA, Mt. Ida). (A leaf has been removed at the cross-hatched area). The zone of the bifarious groove or pubescence is here represented by the leaf mucro which is closely appressed within the boundaries of this same zone, thus giving the series : groove (invagination) — hairs — mucro (evagination). — c, *Leonohebe mooreae* (Ritchie, CHR, Te Waewae). The decurrent pulvinate saddle-shaped leaf buttresses/bases/scars meet centrally at a bifarious strip which is often pubescent. — d, *Leonohebe* sect. *Salicornioides* : 1, shoot ; 2, transverse section. "Stele" stippled, cortex/leaf : not stippled. No sign of a node is visible. The bifarious zone is here represented by a deep groove.

The whipcord and ericoid shrubs of *Leonohebe* sect. *Flagriformes* have internodes which are photosynthetic and very similar in appearance to the leaves, while in *Leonohebe* sect. *Salicornioides* the leaf is entirely confluent with the cortex (Fig. 1, *d*). The absence of any articulation, and thus the ambiguous nature of any “leaf” or “node”, is striking. No visible articulation ever develops even in older shoots, and no “leaf” ever falls. The ring of tissue surrounding the vascular cylinder, the “cortex/leaf”, is eventually obliterated by secondary growth. Describing this shoot structure in *Veronica salicornioides*, HOOKER (1864) wrote: “Leaves closely imbricating and closely appressed to and adnate with the branch [cf. his interpretation of *V. odora*, above], extremely short, opposite pairs connate throughout their length, each pair forming a short narrow ring about 1/20-1/10 inch deep around the branch”. CHEESEMAN (1925 : 782) described *V. propinqua* similarly: “Leaves... lower part adnate to the branch”. However, the structure regarded by HOOKER and CHEESEMAN as the lower, adnate portion of leaf is interpreted by ASHWIN (1961) as stem (cortex), with an unmarked node (“nodal joint obscure... the leaf appearing  $\pm$  continuous with internode below”). This recalls the debate over similar structures in *Salicornia* and other genera of *Chenopodiaceae* (JAMES & KYHOS, 1961). In both families “stem” and “leaf” have been assumed, with no real reason, to be homogeneous and mutually exclusive categories (HEADS, 1984; RUTISHAUSER & SATTTLER, 1989; SATTTLER & RUTISHAUSER, 1990; SATTTLER, 1992; SATTTLER & JEUNE, 1992).

#### 4. INFLORESCENCE.

Inflorescences of *Leonohebe* have all floral bracts opposite and connate, but in the inflorescences of *Hebe* and *Parahebe* phyllotaxis is spiral and sometimes complex. Occasionally the lowest two bracts in a *Hebe* inflorescence are in an “opposite pair”, but then these pair members are not truly opposite, but lie closer together adaxially in a geminate arrangement. Authors such as GUÉDÈS (1979) consider that such geminate organs do not belong to the same node and that they indicate “fusions” such as hypoclades, well-known in the inflorescences, of *Solanaceae*. Racemes of *Hebe* sp. aff. *rakaiensis* from Cobb Valley and Mt Peel, northwest Nelson, are made up of what appear to be pseudowhorls which are more or less disrupted along the rachis (or “dirempted”, to use CROIZAT’s, 1961, term), together with many geminate pairs in a very complex arrangement (pers. obs.). The inflorescence of *Hebe* may thus be the end result of a fundamental morphological reorganisation, involving reduction, recombination and suppression of parts.

#### 5. PERIANTH.

Most contemporary authors (e.g. AIRY SHAW, 1973) use WETTSTEIN’s (1891) classification of *Scrophulariaceae* and place *Veronica* and its allies in subfamily *Rhinanthoideae*. This subfamily is characterised by the posterior corolla lobes covered in the bud by one or both of the lateral lobes. However, in several species of *Chionohebe*, *Leonohebe* and *Ourisia* the posterior lobes regularly cover the lateral lobes. A specimen of *Chionohebe ciliolata* (Mark & Burke, 1967, OTA) has most flowers with the lateral lobes enclosing the two posterior lobes, but in several flowers one lateral is enclosed by the adjacent posterior lobe. Collections of

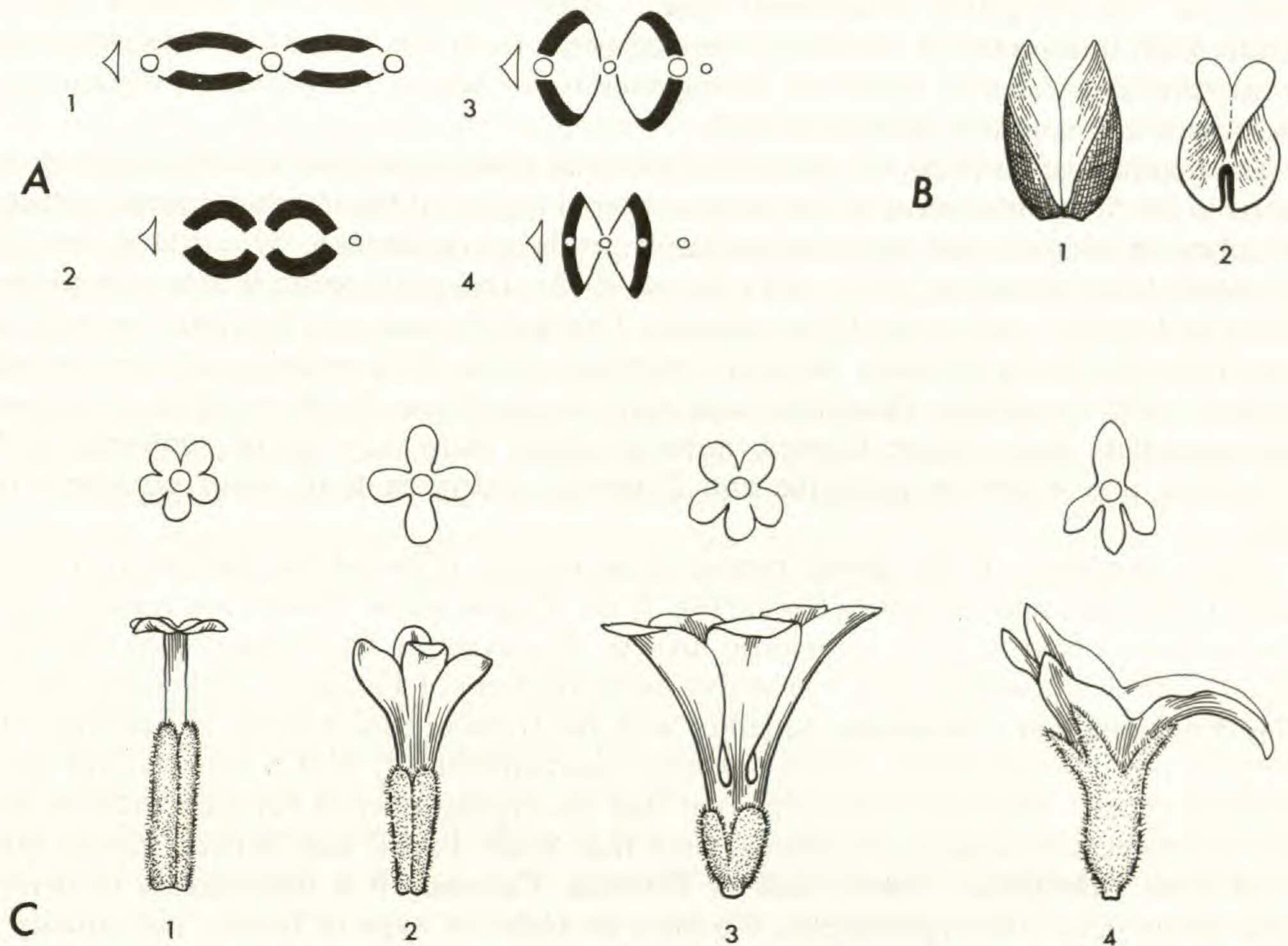


Fig. 2. — A. Cross-sections of fruits (diagrammatic and not to scale). Axis as circle, bract as triangle : 1, *Leonohebe* sect. *Leonohebe* (laterally compressed) ; 2, *L. cupressoides* ; 3, *L. petriei* (“turgid”) ; 4, *Hebe* (dorsally compressed). — B. Capsule dehiscence in *Hebe* : 1, Outer view showing septicial splitting and parting in the median line ; 2, Inner view of one valve and columella with loculicidal dehiscence along the median line. — C. Perianths in the *Hebe* complex : 1, Salverform flower of *Chionohebe* ; 2, Intermediate condition of *Leonohebe* sect. *Leonohebe* ; 3, Funnel-form corolla of *L. densifolia* ; 4, Strong zygomorphy in *Hebe* (*H. acutiflora*, after EAGLE, 1982), with the three anterior lobes and the posterior lobe forming two lips.

*Leonohebe petriei* from the Eyre Mts. (Hedges, 7.3.1987, OTA) have some buds with the lateral corolla lobes enclosing the posterior lobe, while in other buds the posterior lobe encloses the laterals. Plants of *L. densifolia* on Mt Buster (Mt. Ida Range) had the posterior corolla lobes enclosing the lateral lobes in bud (pers. obs.). In buds of New Zealand species of *Ourisia* and also in at least one Chilean species the two posterior corolla lobes overlap the lateral lobes (MOORE, 1961). Thus WETTSTEIN’s subfamilies “deconstruct” in these relictual southern forms with multiple affinities. The position of these genera in *Scrophulariaceae* is complex, as they recombine characters of different groups to such an extent that characters of different subfamilies may appear on the same plant. The group cannot simply be a secondary outlier derived from *Veronica*, which in comparison with the *Hebe* complex appears to have a very homogeneous floral and carpel structure, as well as habit. A detailed study of perianths in the group (SAUNDERS, 1934) revealed the complete absence of marginal veins in the sepals of *L.*

*ciliolata* as “an altogether exceptional case”. Such “exceptions” in southern taxa have generally been interpreted as secondary developments from the “normal” condition, but are here interpreted as relictual variation, dating back to, or before, the primary differentiation of the northern and southern groups as such.

The perianth of all *Hebe* s.s., most *Veronica* and some *Leonohebe* and *Parahebe* species is unusual in the *Scrophulariaceae* as the posterior sepal typical of the family is absent, giving four calyx lobes. In addition, the usual two posterior petals are represented by one large one, giving four corolla lobes (EICHLER, 1875; AIRY SHAW, 1973). The androecium is also reduced to two stamens in *Veronica* and in the *Hebe* complex. This led HOOKER and BENTHAM to include the whole *Hebe* complex in *Veronica*. However, members of the *Hebe* complex such as *Chionohebe*, *Leonohebe* sects. *Leonohebe*, *Densifoliae* and *Apiti*, *L. pauciflora*, *Parahebe trifida*, *P. birleyi* and *P. planopetiolata* have diverse flowers, none of which show any special similarity to those of *Veronica*, and 4-merous perianths and 2-merous androecia both occur elsewhere in the family.

Floral symmetry in the group ranges from regular (*Chionohebe* and many *Leonohebe* species) to strongly zygomorphic (*Hebe*) (Fig. 2, C). Zygomorphic flowers are usually regarded as being derived from radially symmetric flowers. For example HENSLOW (1895) regarded the 5-petal flower of *Chionohebe* as a “probably ancestral form of *Veronica*”. Similarly, SAUNDERS (1934) concluded that *Chionohebe*, together with the tropical east African *V. keniensis* and *V. aberdarica* (see also HEDBERG, 1957), all have characteristically K5C5 flowers and are thus “primitive types”. Here the traditional view that the zygomorphy of *Veronica* must be derived neatly contradicts the equally traditional view that South Pacific and African genera must be derived from “Holarctic” forms such as *Veronica*. Certainly it is unnecessary to derive the regular flower from the zygomorphic *Veronica* or *Hebe* s.s. type of flower, but equally there is no need to see the zygomorphy of *Veronica* and *Hebe* as derived from radially symmetric flowers. Both can be interpreted as alternative symmetries attained during the suppression of parts and reduction of the higher order symmetries of the pre-floral “cone” (CROIZAT, 1961; HEADS, 1984). This process has led to other manifestations of zygomorphy, for example in *Parahebe linifolia* subsp. *brevistylis* where the suture between the stigma lobes runs at 90° to the ovary septum, apparently the result of twisting in the style (GARNOCK-JONES, 1975). This may be compared with developmental and phylogenetic torsions in groups such as orchids, gastropods and vertebrates. Such differential growth within an apparently unitary structure reveals the different structural components which predate the existence of the structure as such, as in a bimetallic strip (FERMOND, 1858). Zygomorphy and torsion are no more or less derived than is the regular, untorted state (which in fact often reveals a telling trace of torsion). Likewise in biogeography, there is no need to invoke any lengthy migrations, either from north to south or vice versa. If a polyphyletic origin of angiosperms on a broad front is assumed (HEADS, 1984), the ancestral complex of the *Digitaleae* may already have been widespread along the northern and southern shores of Tethys when the southern members and their northern relatives differentiated. These views are in general agreement with HONG's (1984) conclusion that it is not possible to derive the southern *Hebe* group from the largely northern *Veronica*, although both are intimately related and share a common ancestral complex.

## 6. BREEDING SYSTEM.

DELPH (1988, 1990) records the majority of species in *Hebe* s.l. as protandrous. *Hebe* group “*Paniculatae*” is protogynous (MOORE, 1973), and so is the apparently unrelated *Leonohebe densifolia* (pers. obs.).

DELPH (1988, 1990) records gynodioecy in some species of *Hebe* sect. *Subdistichae* and sect. *Hebe*, whereas all plants examined of *Hebe* sect. *Glaucæ* had monomorphic, hermaphrodite flowers. Within *Leonohebe*, sections *Buxifoliatae*, *Flagriformes*, *Salicornioides* and *Aromaticæ* are united by uniformly monomorphic flowers, supporting the affinities among them maintained here. Dimorphic flowers only are recorded in *Leonohebe* sects. *Connatae*, *Apiti* (gynodioecious) and *Leonohebe* (dioecious), as well as in *Chionohebe*. *Parahebe*, *Hebe* group “*Paniculatae*” and *Hebe macrantha* all share monomorphic, hermaphrodite flowers, supporting the suggestion made above that these three make up a large *Parahebe*. Thus there is a high degree of correlation between the breeding systems and taxonomic groups based on other characters.

DELPH (1988, 1990) argues that since the family *Scrophulariaceae* has almost entirely hermaphrodite flowers, it follows that floral dimorphism is a derived condition in the *Hebe* group. This deduction seems unwarranted. The most common extant state is not necessarily primitive, and in any case the *Hebe* group is hardly a typical member of the family. As already indicated, it may well have basal affinities. In fact the prevalence of dicliny and dioecy in New Zealand plants is generally assumed to be secondarily derived. This is related to the idea that southern biotas are derived from northern ones, and also to the idea that the first angiosperms had “perfect” flowers. I have attempted to refute both these theories elsewhere (HEADS, 1984, 1989, 1990a). The diclinous condition in angiosperms can be interpreted as inherited directly from the gymnospermous ancestral complex. The so-called “perfect”, bisexual flower found in most angiosperms can then be regarded as a secondary condition.

## 7. DISC.

The floral disc in the *Hebe* complex is well-developed. It has been little studied and may possess taxonomic characters in addition to the ciliate margin, recognised above as a useful marker in *Parahebe*. The discs of *Chionohebe* and *Leonohebe* seem to be generally larger, in relation to the ovary, than in *Hebe*. HOOKER (1864) noted the “rather large” disc of *Chionohebe*, and MOORE & IRWIN (1978) illustrated the disc of *C. pulvinaris* extending to just over half the length of the ovary. In *Leonohebe* the disc is cupular or ringed in *L. petriei*, *L. densifolia*, *L. ciliolata* and *L. cheesemanii*, and *L. haastii* (KIRK, 1896; CHEESEMAN, 1906; SIMPSON & THOMSON, 1943; SIMPSON, 1952). In *L. densifolia* the disc is massive and doughnut shaped, spreading laterally, while in *L. tumida* it is particularly conspicuous and in female buds may reach 1/3 the length of the ovary. In *Leonohebe* disc development in proportion to the ovary is perhaps greatest in *L. cupressoides* (pers. obs.). The colour of the disc may also vary, for example in *L. epacridea* the disc is golden yellow, whereas in *L. cheesemanii* it is short and green.

## 8. OVARY AND FRUIT.

MOORE (1961) noted that plants treated here as *Leonohebe* sect. *Leonohebe*, plus the unrelated *Hebe macrantha* (probably a *Parahebe*), are “difficult to accommodate in *Hebe*... as the capsules are strongly laterally compressed [Fig. 2, A this paper]. In having the septum across the narrowest diameter they resemble *Pygmea*, *Parahebe*, and *Veronica*, [and *Aragoa*] but the septum is long, not short as in those genera... ». The classification followed here does not use these capsule characters at generic level. The capsules of *Hebe* (dorsally compressed with septicidal dehiscence) and of *Veronica* (laterally compressed with usually loculicidal dehiscence) are fairly well-defined, but capsules in *Leonohebe* and *Parahebe* are more varied. For example, capsules in *L.* sect. *Buxifoliatae* range from dorsally compressed, with only slight loculicidal dehiscence, to laterally compressed, obcordate and didymous, with loculicidal dehiscence extending to at least halfway. Capsule dehiscence in *Parahebe* can be either septicidal or loculicidal. As with the perianth aestivation, it is this breakdown of characters which are elsewhere so useful which makes the group so intractable taxonomically.

Trimerous fruits are found regularly in *Leonohebe benthamii* (MOORE, 1961) and in a single collection of *L. ciliolata* (Mark & Adams, 27.12.1967 (OTA) Arthur's Pass). Elsewhere in the family, *Bowkeria* of South Africa seems to be the only genus with a regularly trimerous gynoecium.

## 9. CHROMOSOME NUMBER.

Different ploidy levels are found within single species of *Veronica* (DARLINGTON & WYLIE, 1955), in *Hebe diosmifolia* (MURRAY et al., 1989) and in *Leonohebe odora* (HEADS, 1992). Despite this variation, in other cases chromosome numbers may be very constant in larger groups. A basic number of  $x = 21$  is present in all *Chionohebe*, most *Leonohebe*, and in many *Parahebe* species (incl. *Hebe* group “*Paniculatae*” and *H. macrantha*). In contrast, 47 out of 50 species of *Hebe* s.s. have  $x = 20$  (HAIR, 1967, 1970). *L. benthamii* of the subantarctic Auckland and Campbell Islands is a very distinctive form with the “wrong” number,  $n = 20$ , for its genus and in this case the “incongruent” cytological differentiation is suggestive of a standard biogeographic connection. *L. benthamii* ranges on the southern arc: Auckland Is.-Campbell Is., *Hebe* is best represented to the northeast, while the rest of *Leonohebe* trends westwards. Thus *L. benthamii* represents a pivotal form connecting *Leonohebe* with *Hebe* phylogenetically and biogeographically. Although the species clearly lies in *Leonohebe* through its inflorescence and foliage, it displays “incongruent” links with *Hebe*, notably its chromosome number and its large leaved, orthotropic habit.

## THE “WHIPCORD-SHRUB” HABIT

Members of *Leonohebe* sects. *Leonohebe*, *Flagriformes*, *Salicorniodes* and *Aromaticae* (together equivalent to *Veronica* subgen. *Pseudoveronica* J. B. Armstrong, 1881) form shrubs

with a distinctive habit, similar to that of ericoid shrubs, with small, appressed, scale leaves (Fig. 1, *b*) giving the stems the appearance of plaited leather whipcord.

CHEESEMAN (1914) summed up an interesting aspect of the architecture of these plants : “ The whipcord *Veronicas* are remarkable for the extent to which they resemble plants of very different families. *V. cupressoides* possibly offers as striking an instance as any, for the manner in which the branchlets mimic, as it were, those of a cypress never fails to impress even the most casual observer. We have already seen that *V. tetragona*, when first discovered, was actually figured in mistake for a *Podocarpus*. [Even in modern times expert botanists have identified sterile collections of *Dacrydium biforme* (*Podocarpaceae*) as *Hebe ochracea*]. *V. lycopodioides* has the aspect of several Lycopods with appressed scale-like leaves. Finally, *V. salicornioides* was named on account of the likeness of its branches to those of a species of *Salicornia*. “ The habit of different members of *Leonohebe* is also very similar to that of some *Crassula* species, the only real difference being the succulence of the latter and even this occurs in *Leonohebe salicornioides*. *L. sect. Flagriformes* is vegetatively very close indeed to *C. lycopodioides* of Namibia, and the habit of *L. sect. Leonohebe* closely resembles that of *C. columella* and *C. jacobseniana* of Cape Province, South Africa. Similar structures are also found in many members of *Anacampseros* (*Portulacaceae* — southwest, central and east Africa, southern Australia). BENTHAM (1846) regarded the habit of *V. tetragona* (here *Leonohebe tetragona*) as similar to that of the ericaceous *Andromeda* and *Cassiope*. HENSLOW (1895) wrote that the small appressed leaves of forms placed here in *Leonohebe* are comparable with those of Californian and Japanese *Cupressaceae*, with *Tamarix* (*Tamaricaceae*), and with *Salsola* (*Chenopodiaceae*) of African deserts. Foliar dimorphism similar to that of *Leonohebe* is also found in *Cupressaceae* and *Tamaricaceae*. KIRK (1879) made the accurate and interesting comparison between the branching architecture of *V. armstrongii* and that of certain coralline algae, which recalls DAUGET’S (1986) comparative analysis of tree and coral architecture.

The meaning of these parallels among seed-plant families such as *Cupressaceae*, *Podocarpaceae*, *Ericaceae*, *Crassulaceae*, *Scrophulariaceae*, *Portulacaceae*, *Chenopodiaceae* and *Tamaricaceae* has never been explained. It is suggested below that all these plants have undergone a similar morphogenetic process in which inflorescences, or rather sexualised zones, have been sterilised in some early phase of seed-plant differentiation, to form secondarily vegetative shoots with restriction of actually sexual zones to distal sectors. “ True leaves ” are present only as occasional “ juvenile ” or “ reversion ” foliage, and the scale foliage of most of the plant is made up of floral bracts deprived of flowers.

## 1. LONG AND SHORT SHOOT DIFFERENTIATION.

The distinctive architecture of the whipcord shrubs in *Leonohebe* differs strikingly from that of the orthotropic, large-leaved plants in *Hebe*. The whipcords are characterised by foliage of very small, sessile, connate, scale-like leaves, sometimes with vasculature evident as parallel “ ribs ”, and also by differentiation of plagiotropic long shoots and orthotropic short shoots. Flowering short shoots, often about 10 cm long, tend to arise in two rows on the upper side of decumbent or arching, non-flowering long shoots (Fig. 3, *B*). This arrangement of short shoots gives the branch complexes a dorsiventral structure which resembles the distichous symmetry of plagiotropic, anisophyllous shoots of other *Digitaleae* referred to above, as well

as pinnate structure in many leaves and inflorescences. Long and short shoots in *Leonohebe* are often somewhat recurved at the tips. This recurvature is a further expression of plagiotropy, which in flowering plants is often associated with inflorescence (for example in *Boraginaceae* and *Solanaceae*). COCKAYNE (1909), SIMPSON & THOMSON (1943), SIMPSON (1945) and ASHWIN (1961) have contributed notes on these dorsiventral shoots, while EAGLE (1982) and MARK & ADAMS (1973) provide good illustrations.

## 2. INFLORESCENCE.

In the whipcords and related plants inflorescences terminate short shoots. This arrangement apparently contrasts neatly with that of *Hebe* (Fig. 3, A), in which orthotropic, monopodial branch complexes bear massive inflorescences in lateral position and architecture conforms to RAUH's model (HALLÉ et al., 1978). However, in the whipcords the terminal inflorescence is very small and simple and the vegetative leaves are very similar to the floral bracts, unlike the situation in *Hebe*. This suggests that shoot complexes in the whipcords and their relatives (i.e. *Leonohebe*) are largely sterilised, originally many-flowered, racemes and panicles. As MOORE (1967) observed, in the inflorescences of the whipcords and relatives "the bracts are opposite and almost as large as the leaves, so that the flowers can almost be regarded as solitary and axillary [rather than grouped in a terminal raceme]". The reduction of the inflorescence at least hinted at in these plants is seen clearly in those members of *Leonohebe* and *Chionohebe* which have inflorescences of few-flowered spikelets. This set-up appears to be very different from that of *Hebe*, with its massive racemes, only because in *Hebe* the minute floral bracts differ greatly in morphology and arrangement from the large foliage leaves. If enough bracts were sterilised basally on the *Hebe* inflorescence, and the large vegetative leaves were likewise suppressed and present only as occasional "juvenile" or "reversion" leaves, the "reduction" to a 1-few-flowered inflorescence noted by MOORE would take place. The distinction between "lateral" and "terminal" blurs here, and of course every flower or inflorescence terminates an axis of some sort.

Sterile portions of inflorescences were observed by MOORE (1961) in all four species treated here in *L. sect. Connatae*. This is especially striking in *L. petriei* where the lowermost bracts are sometimes without flowers to a length of 3 cm up the axis. In *L. haastii* var. *humilis* and *L. ramosissima* specimens often have imperfectly developed inflorescences with many empty bracts. In *L. epacridea* only the lowest 2-4 flowers of each spikelet are fully developed.

## 3. DIMORPHIC FOLIAGE.

The strongly dimorphic foliage of plants treated here in *Leonohebe* was first discussed by KIRK (1879, 1896). The so-called "juvenile" or "reversion" leaves in *Leonohebe* are quite distinct from the normal scale leaves. (As POETHIG, 1990, noted: "The use of terms juvenile and adult for different phases of shoot growth implies that these phases are regulated by temporal factors, but it would be just as reasonable to describe these as basal and apical patterns of development..."). "Juvenile" leaves have not been seen in all whipcord species, but in all cases described are "spreading, petiolate, membranous, entire or pinnatifidly toothed



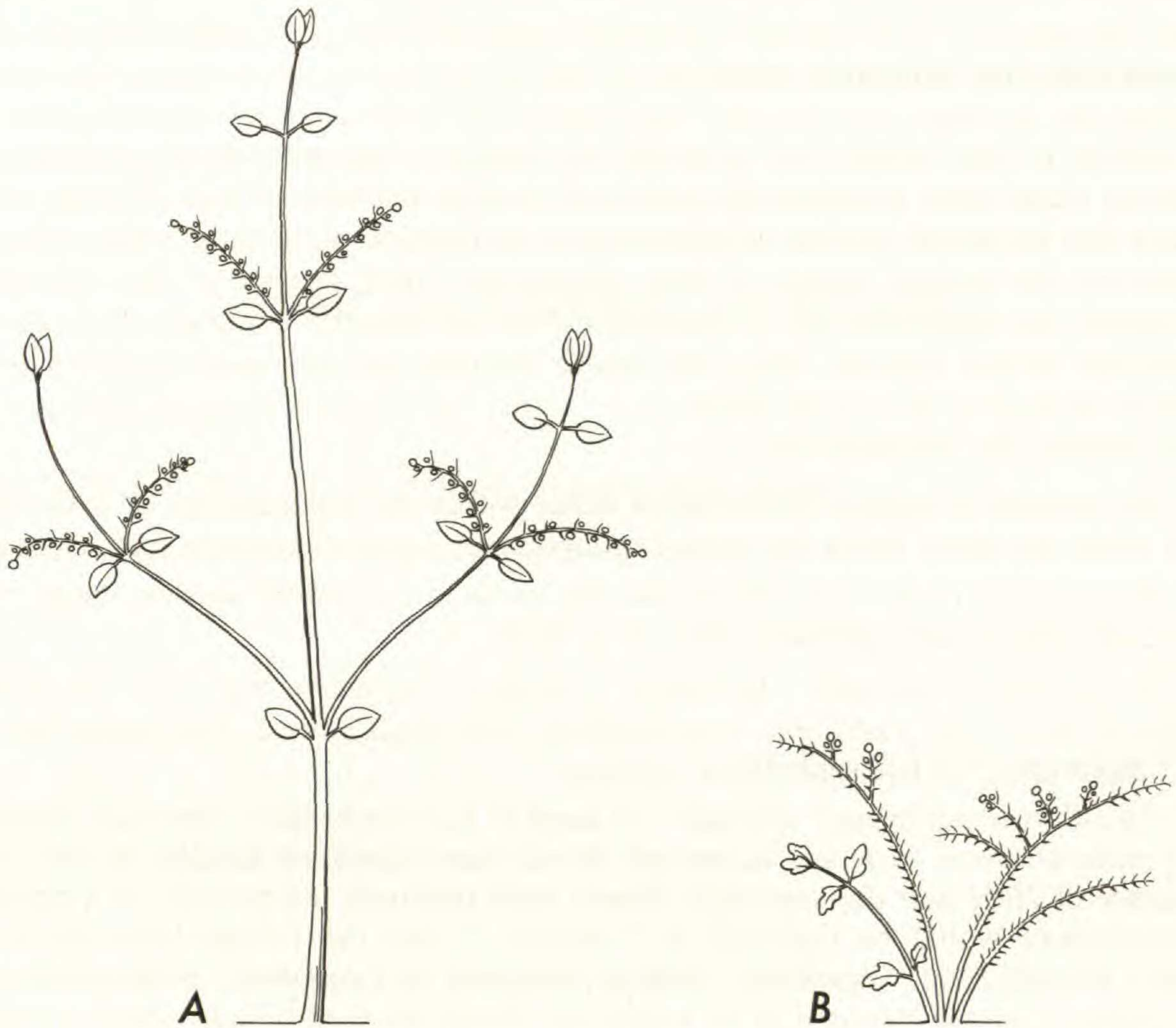


Fig. 3. — Architecture in **Leonohebe** and **Hebe** (diagrammatic) : **A. Hebe**, vegetative axes all orthotropic, with two kinds of foliage : “ vegetative leaves ” and inflorescence bracts. Inflorescence phyllotaxis dirempted from verticillate into complex spirals ; **B. Leonohebe**, axes often plagiotropic, two kinds of foliage : “ reversion ” or “ juvenile ” foliage, and inflorescence bracts, the latter mostly sterile. Flowers restricted to ends of branches. Inflorescence phyllotaxis remains strictly opposite throughout.

or lobed ” (ASHWIN, 1961). CHEESEMAN (1914) gives an excellent illustration showing the “ reversion ” foliage of lobed “ phylloids ” in *L. cupressoides*. In addition, unlike normal leaves, pairs of “ juvenile ” leaves are not connate, and each leaf has a well-marked articulation at the base. The “ juvenile ” foliage thus shows strong parallels with the vegetative foliage of *Parahebe*. Indeed, it occurred to ARMSTRONG (1881) that the lobulate leaves of the “ juvenile ” foliage, “ so often absent, are the true leaves, and that the scale-like productions commonly called leaves are in reality not true leaves... ”. This idea is supported here. ARMSTRONG suggested that the scale leaves of the whipcord shrubs are modified petioles, and GOEBEL (1905 : 353) suggested that they correspond to the leaf-base of the “ juvenile ” leaves. These suggestions are not inaccurate, but both ARMSTRONG and GOEBEL overlooked the virtual identity of the “ scale leaves ” and the inflorescence bracts in these plants. This is in striking contrast to the situation in *Hebe*, where bracts and leaves have quite different size, shape, texture, etc.

#### 4. SUMMARY OF THE WHIPCORD HABIT.

Evolution in seed plants has generally involved a large amount of sterilisation, with sporogenous tissue being progressively restricted to distal portions of axes (HEADS, 1984). The hypothesis that the simple process of inflorescence sterilisation occurred in whipcords accounts simultaneously for several aspects of their architecture. With respect to the “mimicing” of many families, the whipcords may be descended from an ancestral complex which was already architecturally diverse (HEADS, 1985), but whose members all underwent a similar process of sterilisation leading to the ericoid facies.

The process also accounts for :

— the presence of empty, sterile bracts either within the inflorescence or extending some distance down the shoot below the actual inflorescence, as in *Leonohebe* sect. *Connatae* ;

— the similarity of the floral bracts and the leaves in *Leonohebe* (in size, shape, decussate position and connate arrangement), but not in *Hebe* ;

— the presence of strongly “dimorphic” foliage in *Leonohebe* but “not” in *Hebe*. If the inflorescence bracts are taken into consideration, then both genera, like many plants, have clearly “dimorphic”, “heterophyllous” foliage ;

— the inflorescence being “terminal” in most of *Leonohebe* (six of the eight sections), but virtually always lateral in *Hebe*. If enough bracts were sterilised basally on the “lateral” inflorescence of *Hebe* and the vegetative shoots were relatively suppressed, at a certain point the inflorescences would be regarded as “terminal” and the foliage heterophyllous. The so-called “juvenile” or “reversion” foliage common in *Leonohebe*, particularly on basal laterals, seems to be the remnant of an earlier pre-floral phase of foliage which comprises the normal vegetative leaves in *Parahebe* and *Hebe*.

This interpretation of whipcord and similar ericoid architecture in *Leonohebe* may also relate to the architecture of the “divaricating shrubs” which are particularly abundant in New Zealand and Madagascar (HEADS, 1990b). In Madagascan *Didiereaceae* CHOUX (1934) observed structural and morphogenetic parallels between the “cymose” vegetative branching of these plants and the inflorescence architecture of otherwise non-divaricating plants. Investigations along these lines may go some way to accounting for what DAWSON (1988) has accurately identified as “the small leaved shrub problem” in the New Zealand flora — how and why is there such a diversity there of small leaved shrubs with divaricating, whipcord and ericoid habit? The process described here would explain both the “whipcord” and “divaricate” habits as relictual inflorescence structures. It may also explain why the branch architecture of *L. cupressoides*, described by CHEESEMAN (1925) as “divaricating”, can be compared with that of the inflorescence in *Hebe divaricata* (Cheesem.) Ckne. & Allan. Inflorescence sterilisation also accounts for the “ericoid” habit, and is compatible with WATSON’S (1964) interpretation of floral bracts in *Epacridaceae* as reduced flowers.

In *Parahebe ciliata* of New Guinea basal rhizome-like shoots occasionally develop (*A. F. Mark*, 6.6.1967, OTA, Mt. Wilhelm), bearing minute, scale-like, connate, foliar organs resembling foliage of *Leonohebe*. This sterile-inflorescence shoot architecture in basal position may also be found in the “juvenile” stage of *Eucalyptus* (*Myrtaceae*) and in the divaricating

“juvenile” stage of plants such as *Pennantia corymbosa* ( *Icacinaceae*), and may be compared with fertile inflorescences borne basally on the trunk in plants such as *Acrotriche* (*Epacridaceae*), *Goniothalamus* (*Annonaceae*) and *Ficus* spp. (*Moraceae*), some of the latter with geocarpic inflorescences on long “whips”.

## GENERIC AND SUBGENERIC DESCRIPTIONS

**CHIONOHEBE** Briggs & Ehrendorfer (1976 : 1).

— *Pygmea* HOOK f. (1864 : 217) non *Pygmaea* STACKHOUSE (Lichenes).

TYPE : *Chionohebe ciliolata* (Hook. f.) Briggs & Ehrendorfer.

Subshrubs or perennial herbs  $\pm$  woody at base, forming dense cushions of tightly compacted stems, or looser cushions or mats. Leaves entire, sessile, imbricated in chiasmatic pairs, internodes very short. Flowers solitary, sessile or subsessile, lateral near stem tips, with one pair of connate bracts. Calyx with 5 equal lobes. Corolla small, usually  $< 5$  mm diameter, salverform, with  $5 \pm$  equal lobes. Stamens 2, inserted near throat of corolla. Disc annular, rather large. Capsule obcordate and didymous, slightly laterally compressed, splitting loculicidally and septicidally into 4 valves. Chromosome number :  $x = 21$  (HAIR, 1970). Fig. 1,a ; 2,C1.

HOOKER's (1864) description and delimitation of the genus were satisfactory, but BENTHAM & HOOKER (1876) later added *Veronica densifolia*, rendering the group heterogeneous. BENTHAM & HOOKER's decision was followed by ASHWIN (1961) and BRIGGS & EHRENDORFER (1976), but not by CHEESEMAN (1925) who maintained *Pygmea* in the narrow sense of HOOKER (1864). CHEESEMAN noted that the three species of *Pygmea* “differ from *Veronica* [incl. *Hebe* etc.] in the 5- or 6-partite corolla and in the leaves not being quadrifariously arranged”. Some East African species of *Veronica*, as well as species of *Parahebe* and *Leonohebe* have 5-partite corollas, but the observation that the leaves of *Pygmea* are “not quadrifarious”, or “not opposite”, as discussed above under “Phyllotaxis”, is of taxonomic value.

Morphological differentiation within the genus lies largely in the distribution of hairs on the leaf. Hairs may be absent, restricted to the margins, or be present on apical and/or basal sectors (ASHWIN, 1961).

**LEONOHEBE** Heads (1987 : 4).

TYPE : *Leonohebe ciliolata* (Hook. f.) Heads.

Shrubs or subshrubs, foliage small, often scale-like, entire, with varied patterns of pubescence, pairs connate at base and similar to the floral bracts. “Juvenile” or “reversion” foliage sometimes present, often laciniate, pairs not connate, abscission zone well-marked. Floral bracts opposite and connate throughout the inflorescence (inflorescence architecture of

*L. petriei* unclear). Corolla zygomorphic or regular, 4-, 5- or 6-lobed. Stamens 2, occasionally 3, rarely 4. Fruit a 2- or 3-celled capsule. Chromosome number : in 6 sections  $x = 21$ , in sections *Flagriformes* and *Apiti*  $x = 20$  (HAIR, 1967). Fig. 1, 2.

Named in honour of the late Dr. Léon CROIZAT.

1. **Leonohebe** sect. **Densifoliae** Heads (1987 : 4).

TYPE : *Leonohebe densifolia* (F. Muell.) Heads.

Much-branched subshrubs, stems prostrate and rooting proximally, ascending distally, sometimes of "semi-whipcord" form, producing a dense cushion or loose mat, phyllotaxis decussate. Leaves dull olive-bronzy green, entire or trifid, 3-7 mm long, surface  $\pm$  glabrous, margins cartilaginous, lower margins with thick, tooth-like cilia. Flowers lateral, solitary, with a pair of connate bracts, calyx glabrous or with glandular or eglandular pubescence, corolla blue or white, tube short, dilated into broad, funnelform,  $\pm$  regular 5-lobed limb, posterior lobes covered by or covering lateral lobes in bud. Disc cupular. Capsule laterally compressed, obcordate, didymous, with wide septicidal dehiscence and narrow loculicidal dehiscence to at least half-way. Chromosome number :  $x = 21$ .

Usually on a flowering shoot there is a pair of flowers separated by the apical vegetative bud. Sometimes there is only a single flower. The "terminal" vegetative bud always develops concurrently (sylleptically) with the flower or flower pair. BENTHAM (1869) records 6 corolla lobes in Australian material of *L. densifolia*.

Plants of *L. densifolia* on Mt. Buster (Ida Ra.) were found to have protogynous flowers, with the stigmas protruding from the bud (pers. obs.).

The placement of *Parahebe trifida* and *P. birleyi* is problematic. The arrangement of the flowers, their 5-lobed perianth whorls and the large, funnel-form corollas resemble those of *Leonohebe* sect. *Densifoliae*.

2. **Leonohebe** Heads (1987 : 4) sect. **Leonohebe**. *Hebe* Group "Semiflagriformes" Moore (1961 ; 944).

TYPE : *Leonohebe ciliolata* (Hook. f.) Heads.

Low sub-shrubs or loose mats of  $\pm$  strongly quadrifarious "semi-whipcord" branches spreading and ascending from a woody base. Leaves small, entire, similar to bracts, drying black, glabrous on surface, margins with comparatively few, large, tooth - or spine - like cilia, bases connate. "Reversion" foliage (as seen in *L. ciliolata*) irregularly lobulate or pinnatifid. Inflorescence of lateral spikelets crowded around vegetative bud of leader, each spikelet of 1-3 (4) pairs of flowers, flowers rarely solitary and axillary, bracts similar to leaves, all opposite and connate. Plants dioecious. Calyx 4-lobed, corolla white, 4-lobed,  $\pm$  regular (anterior lobe not narrowed). Stamens 2 or very rarely 4. Disc cupular. Stigma sometimes large and frilled. Capsule laterally compressed,  $\pm$  didymous, splitting loculicidally and septicidally into 4  $\pm$  equal valves. Chromosome number :  $x = 21$ .

The unusual sepal vasculature and occasional 3-merous fruit of *L. ciliolata* are mentioned above.

### 3. *Leonohebe* sect. *Connatae* Heads (1987 : 6).

TYPE : *Leonohebe epacridea* (Hook. f.) Heads.

Decumbent or prostrate shrubs, trailing or forming loose mats, leaves small, connate. Inflorescence a terminal head of many spikelets or a simple spike (*L. petriei*), main leaders often not flowering. Bracts similar to the leaves, all opposite and connate (except in *L. petriei*, where inflorescence architecture remains unclear). Plants gynodioecious. Calyx lobes 4-5, long and narrow, corolla white,  $\pm$  regular or with the anterior lobe narrowed, tube long and narrow, limb small, 4-lobed. Capsule turgid, or dorsally or laterally compressed, sometimes didymous. Chromosome number :  $x = 21$ .

HOOKER (1864) placed *Veronica haastii* and *V. epacridea* together as his "Section 5" of New Zealand *Veronica*, here treated as the core of *Leonohebe* sect. *Connatae*. HOOKER regarded the alliance as a "most remarkable form of the genus", and noted the decumbent habit, the short, broad, rigid, densely imbricating leaves in connate pairs, and the flowers in sessile, terminal heads. CHEESEMAN (1925) placed the newly described *V. petriei* in the group and was followed in this by MOORE (1961). This treatment is followed here for lack of any clear alternative. The species is anomalous in either *Hebe* or *Leonohebe*. The wide variation in capsule morphology of the section is illustrated by EAGLE (1982).

### 4. *Leonohebe* sect. *Apiti* Heads (1987 : 7).

TYPE : *Leonohebe benthamii* (Hook. f.) Heads.

Shrubs 15 cm-1 m tall. Leaves to 40 mm long, with downy pubescence on margins and adaxial surface near apex, margins often toothed, leaf pairs connate, "juvenile" foliage unknown. Inflorescence the largest in the genus, a terminal, unbranched spike of at least 10 pairs of flowers, bracts opposite, connate, similar to leaves but smaller. Calyx 4-6 lobed. Corolla bright azure blue, 5-6-lobed,  $\pm$  regular. Stamens 2-3. Capsule 2-3-celled. Chromosome number :  $n = 20$ .

*Apiti* is a Maori word signifying something confined ; a friend ; to lay a spell on ; to attack ; to put together ; to place side by side ; and to supplement.

### 5. *Leonohebe* sect. *Salicornioides* Heads (1987 : 7).

TYPE : *Leonohebe salicornioides* (Hook. f.) Heads.

Shrubs 10 cm to 1 m tall, shoots orthotropic or prostrate and rooting, stems often soft and fleshy, terete to slightly tetragonous. Scale-like leaves small, connate, nodal joint not evident, leaf tissue continuous with cortex of "internode" below. Stem with glabrous, bifarious

grooves. "Reversion" leaves rare, larger than ordinary leaves, cuneate-spathulate, spreading, irregularly lobulate, node clearly marked, leaf-bases not connate but confluent into 2 decurrent ridges enclosing each stem groove. Inflorescence a terminal head of spikes, each spike with up to 6 pairs of flowers, bracts similar to the scale-like leaves. Calyx with 2 anterior lobes  $\pm$  completely fused into broad, obtuse lamina. Corolla white, lilac or mauve, 4-lobed, lobes  $\pm$  equal, tube short. Disc lobed, to 1/2 length of ovary. Capsule dorsally compressed. Chromosome number :  $x = 21$ .  $n = 21$  in *L. salicornioides* and *L. annulata*. *L. armstrongii* is tetraploid, and *L. ochracea* is an aneuploid variant :  $2n = 124$ .

This distinctive section differs from sect. *Flagriformes* through the absence of a node, the fused anterior calyx lobes and the basic chromosome number  $x = 21$ .

#### 6. *Leonohebe* sect. *Aromaticae* Heads (1987 : 8).

TYPE : *Leonohebe cupressoides* (Hook. f.) Heads.

Rounded bushes to 2 m high, older branches with dark brown, flaking bark, final branchlets  $\pm$  1 mm diameter,  $\pm$  glaucous to dark green, releasing a resinous aroma when crushed. Foliage dimorphic, both kinds with node evident. Scale-like leaves narrow-triangular, barely connate, internodes much longer than leaves. "Reversion" leaves with irregular or  $\pm$  opposite lobes, not connate. Inflorescence a terminal, 6-8-flowered spike, bracts similar to scale-like leaves. Calyx with two anterior lobes fused into a single segment, two posterior lobes similarly fused. Corolla white or lilac, 4-lobed. Disc yellow, extending to 1/2 length of ovary. Capsule  $2 \times 1$  mm, somewhat laterally compressed, grooved at septum, emarginate at apex. Chromosome number :  $n = 21$ .

HOOKER's (1864) *Veronica* "Section 4" comprised a broad group of "whipcord" shrubs. *L. cupressoides* was placed in this group, but set apart from all the other species. CHEESEMAN (1925) followed a similar course, splitting off a group treated here as *L.* sect. *Leonohebe*, and also separating *L. cupressoides* — "a very remarkable species" — from the others. Its distinctive odour, strict orthotropy, slender branchlets, long internodes, glabrous rachis, fused anterior and posterior calyx lobes, and very small, laterally compressed capsule all distinguish this plant from *L.* sects. *Flagriformes* and *Salicornioides*. The lateral compression of the capsule resembles that of *L. pauciflora* (sect. *Buxifoliae*), *L. densifolia*, *Chionohebe* and *Parahebe*.

#### 7. *Leonohebe* sect. *Flagriformes* Heads (1987 : 8).

TYPE : *Leonohebe hectorii* (Hook. f.) Heads.

Small shrubs, sometimes  $\pm$  cushion-shaped, leaders  $\pm$  oblique to prostrate and rooting and forming a mat, bearing numerous orthotropic flowering shoots in 2-4 rows on the upper surface. Foliage often strongly dimorphic : 1. scale-like, similar to the inflorescence bracts, small, thick, deltoid-subulate, often mucronate and sometimes with parallel longitudinal vasculature evident as ridges, pairs connate, node evident. 2. larger, spreading, irregularly lobulate-pinnatifid to laciniate, pairs not connate, node evident. Inflorescences terminal,

simple, 4-14 flowered spikes, bracts all opposite and connate, similar to the scale-like foliage. Calyx lobes 4, free. Corolla white or lilac, 4-lobed, zygomorphic, anterior lobe often narrowed. Disc to 1/4 length of ovary. Capsule dorsally compressed. Chromosome number :  $x = 20$ .

Collections of *L. hectorii* from the Eyre Mts. (Heads, 7.3.1987, OTA) have the anterior corolla lobe folded conduplicately in the bud, completely enclosing the style prior to anthesis, as in members of sect. *Buxifoliatae*.

#### 8. *Leonohebe* sect. *Buxifoliatae* Heads (1987 : 10).

TYPE : *Leonohebe odora* (Hook. f.) Heads.

Prostrate to erect shrubs to 2 m high, final branches dark or bronzy green, sometimes flexed plagiotropically. Young leaf pairs coherent by the margins until nearly fully grown, or not coherent, bud sinus broad, shield-shaped or obtusate-rhomboid, or elliptic with truncate or cordate base barely connate below, leaf-scar raised on pulvinate base. Irregularly lobed "reversion" foliage very rare. Inflorescence terminal or intercalary, of simple spikelets or branched spikes, each spike with 1 to many pairs of flowers. Bracts opposite and connate throughout, at least lowermost bracts  $\pm$  leaf-like. Calyx with anterior lobes fused or not. Corolla white or lilac, 3-4-lobed with anterior lobe absent or narrowed or conduplicately folded and enclosing style until anthesis, or corolla 5-lobed and  $\pm$  regular with 2 posterior lobes. Disc present. Capsule dorsally compressed or laterally compressed and  $\pm$  didymous. Chromosome number :  $x = 21$ , some populations of *L. odora* are tetraploid, *L. mooreae* is hexaploid and *L. masoniae* is aneuploid :  $n = 59$ .

This section is revised in HEADS (1992).

#### HEBE Commerson ex A.L. de Jussieu (1789).

TYPE : *Hebe magellanica* J. F. Gmel. (= *H. elliptica* (Forst. f.) Pennell).

Prostrate or erect shrubs or trees to 12 m tall with trunk to 1 m in diameter. Leaves of each opposite pair connate in bud by the margins, not diverging until almost fully grown. Inflorescences many-flowered lateral racemes, bract phyllotaxis spiral, complex, lowermost bracts sometimes opposite but not connate, whole inflorescence sometimes tending to distichy. Bracts much smaller than leaves and with different shape and texture. Calyx 4-lobed, anterior lobes fused or not. Corolla white, reddish purple, or bluish purple, 4-lobed, anterior lobe often narrow, posterior lobe often forming an erect upper lip with the other three lobes deflexed and together forming a lower lip. Capsule dorsally compressed. Disc present. Basic chromosome number  $x = 20$ . Aneuploid variants : *H. vernicosa* ( $n = 21$ ), *H. macrocarpa* var. *brevifolia* ( $n = 59$ ), *H. topiaria* ( $n = 61$ ). Diploidy ( $2n = 40$ ) and tetraploidy ( $2n = 80$ ) occur in all sections. Hexaploidy ( $2n = 120$ ) occurs, together with diploidy and tetraploidy, in Ser. *Occlusae* and Sect. *Subdistichae* only.

1. **Hebe** sect. **Subdistichae** Heads (1987 : 11).

TYPE : *Hebe diosmifolia* (A. Cunn.) Ckne. & Allan.

Prostrate to erect shrubs, leaves rather rigid, small for the genus, generally dark or bronzy green, sometimes glaucous, phyllotaxis tending to distichous. Sinus between the leaves in bud long, narrow, acute, petiole distinct and lamina cuneate to base. Inflorescence tending to branch, lowermost bracts sometimes opposite. Corolla white or pale blue.

MOORE (1967) described the " Gothic " arch of the sinus seen laterally at the base of the leaf pairs. The lowermost inflorescence bracts are sometimes opposite, and also recalling *Leonohebe* and *Parahebe* is MOORE's (1961) report that : " in rather pampered garden plants of *H. colensoi* and *H. vernicosa*... the usually vegetative tip tends to become reproductive ". In this section the lamina is glabrous except for the margins and midrib in *H. canterburiensis* and the entire leaf in *H. insularis* (Three Kings), in which the pubescence recalls that of *H. pubescens* (Coromandel-Barrier Is.) (sect. *Hebe* ser. *Hebe*) and the Chatham Is. group of sect. *Hebe* ser. *Occlusae*. Several members of the section have a similar habit to that of *Leonohebe* sect. *Buxifoliatae* and the two groups are often confused, sometimes on mixed sheets.

Branching in the inflorescence is very rare in *Hebe*, but is seen in several species of this section. It is known elsewhere in the genus only in the Kennedy Bay population of *H. macrocarpa*.

2. **Hebe** sect. **Glaucæ** Heads (1987 : 11).

TYPE : *Hebe pinguifolia* (Hook. f.) Ckne. & Allan.

Decumbent to erect shrubs often with a woody stock, leaves glaucous, sometimes fleshy, leaf bud usually with the sinus totally occluded, inflorescences usually compact or narrow, with flowers sessile or only shortly pedicellate, lowermost bracts opposite or not. Corolla white, blue or purple.

The section has been recognised as a group by all authors from the time of HOOKER (1864) on. MOORE (1961) provided a useful division within sect. *Glaucæ*, with one group having flowers quite sessile and lowermost bracts opposite, and one group with short pedicels and lowermost bracts not opposite.

The capsules of *H. amplexicaulis* and *H. allanii* and *H. pareora* are didymous (MOORE, 1961 ; GARNOCK-JONES & MOLLOY, 1982) — an unusual character in *Hebe*. The lamina (except the margin and midrib) of members of the section is glabrous except in *H. allanii*, treated here as a form under *H. amplexicaulis*.

3. **Hebe** sect. **Hebe**.

TYPE : *Hebe magellanica* J. F. Gmel. (= *H. elliptica* (Forst. f.) Pennell).

Prostrate to erect shrubs or trees, leaves bright green, not glaucous. Inflorescence a comparatively massive, many-flowered raceme. Calyx lobes 4, free. Corolla white to dark purplish blue or red. Disc present.



MOORE (1961) observed that in some species of *Hebe* the leaf-margins of an opposite pair “remain in close contact throughout their length [sect. *Hebe* ser. *Occlusae* and sect. *Subcarnosae*], but in those where a true petiole develops early the two leaf bases are separated in the bud by a distinct gap or sinus”. MOORE cites PETRIE’s early use of this sinus as diagnostic at species level, but her own study is the first to really exploit the possibilities of this character. In particular her recognition of ser. *Hebe* (her “*Apertae*”) distinct from ser. *Occlusae* is quite novel. The two groups are difficult to distinguish morphologically, but it should be noted that the sinus character correlates with vicariant main massings, as ser. *Hebe* is mainly a southern group, ser. *Occlusae* a northern one. The two groups probably include each other’s closest relatives (cf. MOORE, 1961), and are taken here to comprise sect. *Hebe*. However, ser. *Occlusae* warrants further study — a “*Hebe traversii* complex” may turn out to be a more useful concept.

**Sect. *Hebe* ser. *Hebe*.**

TYPE : *Hebe magellanica* J. F. Gmel.

Southern plants with a broad-square or narrow bud sinus.

This series is mixed with ser. *Occlusae* and sect. *Subdistichae* by CHEESEMAN (1925) in his species 1-46. The “Gothic” arch of the sinus is shared with sect. *Subdistichae*. The lamina (except midrib and margins) is usually glabrous, except in the Coromandel population of *H. pubescens*, which usually has the whole undersurface (at least when young) clad in soft, villous hairs. This can be compared with the pubescence of the Three Kings and Chatham Is. species of *Hebe*. Such form-making along tracks near present-day coasts vicariates with inland (to montane) forms such as *H. salicifolia*.

**Sect. *Hebe* ser. *Occlusae* Heads (1987 : 11).**

TYPE : *Hebe macrocarpa* (Vahl) Ckne. & Allan.

Northern plants without a sinus in the bud.

Members of this large group are found mainly in the northeast of New Zealand, while members of ser. *Hebe* range to the south and west.

GARNOCK-JONES (1976a) suggested that ser. *Occlusae* may be divided into two “sections”, one a group of northern, predominantly diploid species, with large leaves ( $> 3 \times 1$  cm) and the other a group of southern, predominantly polyploid species with smaller leaves. However, *H. stricta* and *H. macrocarpa*, northern large-leaved species, are tetraploid or hexaploid, *H. parviflora* includes both diploid and tetraploid forms, and *H. traversii* (southern, small-leaved) is diploid. Thus a split along these lines may be possible, but cannot be simple.

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